

females are harvested after an average of three years of spawning (age 5 yrs) and at only ~50% of their potential length and therefore, with much lower reproductive output. A larger size enables females to produce more oocytes because fecundity is correlated to body size (e.g., a 1400 mm female Gulf corvina could produce over 2,500,000 eggs per batch). Additionally, older females have been shown to produce higher quality oocytes and larvae that are more resistant to starvation and grow faster than those produced by younger fish (Berkeley et al. 2004).

The distribution of oocyte diameters and the presence of several developmental stages within samples indicate that Gulf corvina is a multiple batch spawner (Calliet et al. 1996; Macchi 1998). Multiple stages were present in all samples with 57 of 58 samples consisting mostly (>75%) of oocytes of one developmental stage. The presence of multiple developmental stages within a single ovary indicates that these are indeterminate spawners (Hunter et al. 1985). Also, some females captured in the morning (i.e., before spawning), showed clear histological evidence of daily spawning via the presence of both recent (<12 hr) POF's and newly hydrating oocytes. Therefore, total annual fecundity is not fixed at the beginning of the reproductive season, and immature oocytes continually mature and are spawned throughout the reproductive season (Hunter et al. 1992). In order to estimate total annual fecundity for multiple batch spawning fishes, information on both the number of times an individual spawns in a reproductive season and the percent of oocytes that are resorbed are necessary (Hunter et al. 1985). For this, a tagging study is needed to determine the number of times a female returns to the estuary to spawn in a single year.

Batch fecundity estimates ranged from 240,394 to 1,219,342 eggs with a mean of 684,293 eggs per spawn. Román-Rodríguez (2000) estimated a similar BF range of 250,000 to 808,000 eggs per batch for *C. othonopterus*. However, only nine fish were sampled in the previous study, which may have resulted in a narrower range. Our fecundity estimates differed significantly between years, with 2010 having a significantly greater fecundity. This could be due to the El Niño event that occurred from May 2009 through April 2010. During and after El Niño events significant increases in zooplankton biomass have been documented in the Gulf of California (Jiménez-Pérez and Lara-Lara 1988; Lavaniegos-Espejo and Lara-Lara 1990; Sánchez-Velasco et al. 2000). Augmented zooplankton biomass would increase the productivity of the area and likely result in a greater abundance of food for *C. othonopterus*, which would provide more energy for reproduction. Fifty percent of females mature at just less than 300 mm but the fishery targets fish greater than 600 mm. Therefore, a complete range of mature females was not used to estimate BF and fecundity is not known for smaller mature females. Fishery-independent sampling of smaller samples is needed in order to understand the correlation between BF and length at the onset of maturity.

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## Recent Mass Mortality of *Strongylocentrotus purpuratus* (Echinodermata: Echinoidea) at Malibu and a Review of Purple Sea Urchin Kills Elsewhere in California

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**Abstract.**—Mass mortalities of intertidal purple sea urchins, *Strongylocentrotus purpuratus* occurred at Malibu Lagoon State Beach, California, in 2010 and 2011. Both events followed the first heavy rain of the season, and coincided with the illegal breaching of a coastal lagoon. Osmotic shock from low-salinity lagoon water, the likely cause of death, may have acted jointly with stress from subaerial exposure during especially low tides. Massive die-offs of purple sea urchins have occurred at other localities, usually after natural conditions created lethal levels of osmotic or thermal stress, or because of human efforts to harvest or to eradicate the species. Annually recurring lagoon ruptures at Malibu, combined with predation by western gulls, can have a profound impact on the local population of *S. purpuratus* and on intertidal ecology.

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### Introduction

At sunrise on October 9, 2010, in Malibu, California, dignitaries inaugurating Surfrider Beach (Malibu Lagoon State Beach) as the first World Surfing Reserve unexpectedly encountered more than 10,000 freshly killed *Strongylocentrotus purpuratus* (Stimpson, 1857) stranded at the tideline (Ralston, pers. comm.). The cause of their death was still undetermined a year later, after another, less severe mass mortality of sea urchins occurred at the same locality. What killed the sea urchins at Malibu in these two successive years, and what might cause mass mortalities of *S. purpuratus* elsewhere in California?

*Strongylocentrotus purpuratus* has a broad range of tolerance for thermal, osmotic, and anaerobic stress as evidenced by its extensive distribution from Shelikof Island, Alaska to Isla Cedros, Mexico, and from the mid-intertidal to 30 m (exceptionally to 161 m) depths (Sagarin and Gaines, 2002; Lambert and Austin, 2007; Lester et al., 2007; Pearse and Mooi, 2007; Ebert, 2010, and pers. comm.). Yet its habitat sometimes imposes stresses that exceed the species' tolerance, resulting in die-offs of purple sea urchins. Past events of this sort generally have been attributed to radical alterations in salinity or temperature, or disease. Since the same factors could have been responsible for the mass mortality at Malibu Lagoon, I discuss the specific tolerances and vulnerabilities of *S. purpuratus*, and review the causes of prior massive kills. Based on that information, I offer a hypothesis regarding the events at Malibu.

Individuals of *S. purpuratus* are weakened or killed by exposure to extreme temperatures or salinities (Schroeter, 1978). They cannot survive for more than 3 h in seawater that is  $\leq 60\%$  ( $\sim 20\%$ ) or  $\geq 120\%$  ( $\sim 39\%$ ) in concentration, and they die after 4 h, if exposed to temperatures more extreme than 1.9 to 23.5 °C (Farmanfarmaian and Giese, 1963; Giese and Farmanfarmaian, 1963; Burnett et al., 2002); vulnerability to elevated temperatures may shape the southern range limit of *S. purpuratus* (Ebert, 2010). Like

other echinoids that have been tested, purple sea urchins probably can tolerate, for hours or days, mild to moderate hypoxia ( $> 0.5 \text{ ml DO L}^{-1}$ ) or elevated levels of hydrogen sulfide, but cannot survive severe hypoxia or anoxia ( $< 0.5 \text{ ml DO L}^{-1}$ ) (Thompson et al., 1991; Riedl et al., 2012). They withstand hypoxic conditions by curbing their oxygen consumption and exploiting anaerobic respiration, and individuals that are emersed can absorb oxygen from the air (Johansen and Vadas, 1967; Burnett et al., 2002).

Although *S. purpuratus* tenaciously grips the substrate to avoid dislodgement (Denny et al., 1985; Denny and Gaylord, 1996), large numbers of individuals have been torn from rocky reefs by wave surge under particularly harsh winter-storm conditions. Abrupt changes in salinity during storms have also proved lethal to *S. purpuratus*. Ebeling et al. (1985) reported that an extensive "urchin front" off Santa Barbara, California, was decimated by surge during a violent storm in 1983. A severe storm in 1938 ruptured a river levee, releasing a massive volume of fresh water into Newport Bay, California, killing animals as far as 3.2 km from the mouth of the bay (MacGinitie, 1939:685). Purple sea urchins were "among those animals which were most obviously devastated by the storm... hundreds of the tests were washed up on the beach or fell to the bottom between the rocks where they were visible at low tides as whitish patches. Even at the lowest tide not a single sea urchin could be seen on the rocks." Despite the massive fatalities, the population nearly recovered within a year. A flash flood in 1977, which deluged the rocky shore at Corona del Mar, California, killed 90.5% of *S. purpuratus* (a decrease of 60 per  $\text{m}^2$ ) in the mid- and lower intertidal of the affected area (Littler and Littler, 1987). Windrows of urchins were found cast onto the beach two days after the storm, at which time salinity measured a record low 23.5‰. Sousa (1979) found a reduced density of *S. purpuratus* and crabs in an intertidal boulder field near Santa Barbara, California, where freshwater runoff from a seasonal creek reached the intertidal. In 1973, at the same locality, Schroeter (pers. comm.) observed that "a single large rainstorm caused freshwater discharge that ponded in the lower portion of the boulder field creating a purple sea urchin bouillabaisse sans fish and near complete mortality. All of the urchins that were at a slightly higher elevation (~0.1–0.2 feet higher) appeared to be unaffected." A similar rain related die-off was thought to have occurred at Sunset Bay, Oregon, where slow recovery of the population of *S. purpuratus* was anticipated (Ebert and Grupe, 2008).

Thermal stress has also caused its share of mass mortalities of *S. purpuratus*. Hedgpeth and Gonor (1969:94) recorded internal body temperatures of *S. purpuratus* "...of 26° C...in beds of urchins exposed to the sun, and maximums of 27° C. to 30° C. in some urchins. Successive days of this type of heating at low tide for periods of three to five hours led to a heat kill at the study site and other areas along the central Oregon coast, with many urchins dying in each place." They also noted that similar die-offs of *S. purpuratus* had been observed at other localities in Oregon for years. A mass mortality event coincident with water temperatures  $> 24^\circ \text{C}$  decimated *S. purpuratus* at False Point, La Jolla, California, in the summer of 1971. Sea urchins did not reappear there until the winter of 1973, following the successful settlement of juveniles (Ebert, 1983). In another instance, several hundred dead *S. purpuratus* were found after a series of minus tides at Newport, California, and the mortality event was tentatively attributed to 24 to 27 °C water temperatures (So, 2006).\*

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\*So, H. 2006. Officials suspect weather played a role in mass sea urchin deaths. Los Angeles Times. August 3, 2006:B.3. Available from <http://articles.latimes.com/2006/aug/03/local/me-seaurchin3> via the Internet. Accessed 2 November, 2012.

In addition, disease outbreaks have been reported among *S. purpuratus* in California, and increasingly frequently among other echinoid species, during the last several decades (Ward and Lafferty, 2004). In the 1970s, infected *Strongylocentrotus franciscanus* (A. Agassiz, 1863) were first found near San Diego, and afterwards at localities off central California (Johnson, 1971; Pearse et al., 1977). Affected animals could not grip the substrate, their ossicles deteriorated and spines detached, and they died within several months. However, the affected populations recovered (Pearse et al., 1977; Pearse and Hines, 1987). In the same region, Gilles and Pearse (1986) found a low incidence of diseased *S. purpuratus*. Lester et al. (2007) documented two different pathologies of infected *S. purpuratus*, presumed to represent distinct diseases, in an intertidal survey spanning central California to Baja California, Mexico in 2004. They found that disease prevalence was positively correlated with temperature but not with population density, leading them to suggest that “If thermal stress does increase host susceptibility, disease in *Strongylocentrotus* species could increase with global warming and increased human impacts along the coast” (Lester et al., 2007:322). Yet another source of mortality, thus far manifested by a single, massive die-off of *S. purpuratus* and less drastic damage to *S. franciscanus*, appears to have been produced by an unidentified toxin from a harmful algal bloom in northern California during 2011 (Jurgens, pers. comm.).

With respect to the mass mortalities at Malibu State Beach, California, in 2010 and 2011, I propose for reasons discussed herein that the sea urchins were killed by fresh water released through a breach in a rain-swollen coastal lagoon, which drastically lowered salinity in the intertidal zone. I also suggest that damage from osmotic stress was probably aggravated by subaerial exposure of the animals during low tides, and possibly by their burial under transported sediment.

## Materials and Methods

### *Study Site*

At present, Malibu Lagoon is an ecologically dysfunctional seasonal estuary. Roughly 0.1 km<sup>2</sup> in area, it channels water from a surrounding 284 km<sup>2</sup> drainage basin into Santa Monica Bay (Figure 1A). The lagoon is the remnant of a previously much larger estuary and wetland that, after 1900, was drastically reduced in size by repurposing natural habitat for ranching and urban development, and by constructing a dam, sewage treatment plant, railroad, and highway, all of which disrupted the estuarine lagoon system and the ecology of its biota (Ambrose and Orme, 2000). As a result “...the Malibu estuarine lagoon is no longer a natural system because, although stream floods and storm waves may sometimes reassert dominance there are now so many constraints imposed by human activity” (Ambrose and Orme, 2000:2–4; Schwarz and Orme, 2005).

The lagoon changes seasonally from closed lagoon to estuary. Typically during the summer and fall, drifting sediment forms a sand bar that blocks the estuary’s mouth, allowing fresh water from the City of Malibu and Malibu Creek to accumulate in the embayment (Ambrose and Orme, 2000). Floods from winter storms rupture the sand bar, flushing brackish water, sediment, biota, nutrients, and human and animal waste from the lagoon through the breach (Ambrose and Orme, 2000; Schwarz and Orme, 2005). Usually throughout the spring, an opening in the sand bar is maintained by outflow from Malibu Creek, and by tidal flow that can move approximately 100,000 m<sup>3</sup> of water through the mouth in single tidal cycles (Ambrose and Orme, 2000). The volume may double during extreme weather conditions when the lagoon fills to the highest level (Ambrose and Orme, 2000; Schwarz and Orme, 2005). Seaward of the sand bar there is a



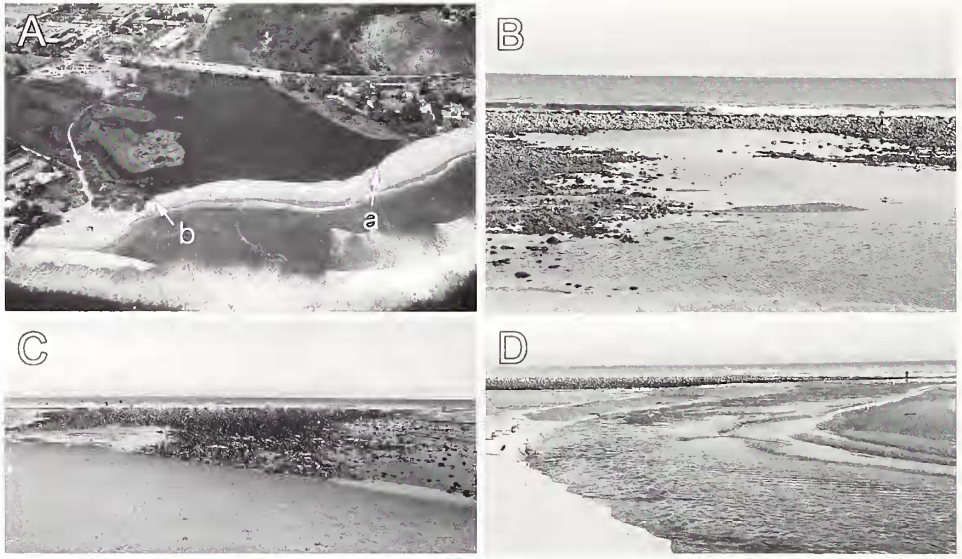


Fig. 1. Malibu Lagoon State Park and its contiguous intertidal reefs. A) Aerial view of Malibu Lagoon at high tide on September 5, 2008. Arrows indicate approximate positions of breaches through the sandbar in 2010 (a), and 2011 (b). B) Portion of Basin Reef at low tide on October 27, 2011, showing water pooled in the reef's shallow central depression, and Santa Monica Bay in the distance. C) Bird Reef in its entirety at low tide on October 15, 2011. Sediment near the cobbles was transported and redistributed after the breach on October 6, 2011. D) View of Bird Reef on October 27, 2011, showing remnants of a channel through the sandbar, which was excavated by outflow through the breach. (Photo A, courtesy H. Burdick, Los Angeles Waterkeeper).

wave-washed shelf composed of cobbles and sediment, part of which is exposed subaerially at low tides. Algal cover on the shelf is quite sparse compared to the dense growth of kelp and other macroalgae in the subtidal zone.

Beginning in 1984, the California Department of Parks and Recreation (DPR) mechanically breached the lagoon when water levels were high, in order to avert septic system failures in the adjacent Malibu Colony and Civic Center (Ambrose and Orme, 2000). The agency deliberately opened the sand bar near the western side of the lagoon in an effort to facilitate pedestrian access to the beach and to avoid spoiling the surf break. Breaching the bar at the lower semidiurnal tide maximized the grade between lagoon and ocean, maximized the amount of sediment flushed out, and increased the period that the lagoon remained open. DPR suspended the practice in 1997, when it was deemed a potential threat to tidewater gobies (*Encyclogobius newberryi* Girard, 1854) that had been reintroduced in the lagoon (Swift et al., 1993; Ambrose and Orme, 2000). Since that year, despite a legal prohibition, the western end of the sandbar has repeatedly been breached, usually but not always when a natural breach was imminent (Pfeifer, pers. comm.), by individuals "concerned with lagoon eutrophication and the quality of the surfing environment" (Schwarz and Orme, 2005:97).

### Methods

Supratidal and intertidal zones at Malibu Lagoon State Beach were surveyed to investigate the origin of sea urchin kills and to gauge the impact of lagoon breaches. Information was gathered opportunistically, since mortality events were unanticipated.



By necessity, features of the biota and habitat preceding the events were determined based on the observations of local observers and from recordings made by automated monitoring equipment. After the events on 2010 and 2011, the effects and magnitudes of the kills were assessed by counting the numbers of freshly dead sea urchins deposited in beach wrack, and by measuring their body size. In addition, the population density and size of surviving animals were quantified by counting and measuring living sea urchins along intertidal transects.

*Strongylocentrotus purpuratus* was surveyed at two adjacent “reefs,” i.e., platforms of cobbles and sediment on the intertidal shelf, which were separated by a channel. Basin Reef encloses a central, sandy depression and is seaward of the middle of the lagoon (Figure 1B). Bird Reef is near the western side of the lagoon and to the east of another reef on Malibu Point (Figures 1C, D). Ruptures in the sandbar closing the lagoon directed lagoon water toward Basin Reef in 2010, and toward Bird Reef in 2011 (Figure 1A).

After the kill in 2010, I visited Malibu Beach on two different days to examine dead animals that had accumulated in beach wrack and to assess their numbers: October 14 near slack tide, one week after the first mass mortality, and during low tide on October 23 (0 cm tide; referenced to Mean Lower Low Water (MLLW)). I also laid transect lines to measure the density of surviving sea urchins at Basin Reef and Bird Reef on November 5 and 7 (during  $-30$  cm tides). At each 15 m long transect line, I counted animals that were exposed, or found under easily turned rocks, in fifteen  $0.25$  m<sup>2</sup> quadrats spaced at 1 m intervals.

One week after the kill in 2011, I examined the shore, looking for dead animals during low tide on October 13 (+9 cm tide), and once more on 15 October (+18 cm). I also surveyed the number of sea urchins in transects at Basin and Bird reefs on October 26, 27, and 28 ( $-30$ ,  $-37$ , and  $-34$  cm). Additionally, on October 27, 2011, I recorded the size of *S. purpuratus* at Basin Reef and Bird Reef. Calipers were used to measure the test diameter of sea urchins that survived the event, which were collected from fifteen  $0.25$  m<sup>2</sup> quadrats at one of the multiple transects on each reef. On October 13, 2011, I similarly measured the test diameters of urchins that died during the event, which were collected arbitrarily from wrack on the high water line, in order to compare their size to that of live animals in the intertidal zone.

Stranded sea urchins were also examined for signs of physical damage in order to determine the cause of their death. Diseased *S. purpuratus* have distinctive lesions in the integument, discoloration of the test, or “bald” patches that are bare of spines (Lester et al., 2007). Lobsters consume purple sea urchins in their entirety, sea stars denude them of spines, and fishes damage them in a characteristic manner (Tegner and Dayton, 1981). Avian predators break open the dorsal or ventral surface of the test, or rupture the peristomial membrane and remove Aristotle’s lantern (Hendler, 1977; this report). In contrast, individuals exposed to lethal levels of osmotic stress initially become immobile, and remain virtually intact after they die (Giese and Farmanfarmanian, 1963).

In 2010, records of water level and water quality in Malibu Lagoon were used to infer the timing of the breach and properties of the water that was released. Water elevation relative to NAVD88 and water quality characteristics were recorded at several stations in the lagoon by Heal the Bay using YSI600XLM sondes, attached 6 to 15 cm above the benthos, which logged data at 30 min intervals (2NDNATURE, 2010). Data from the probes that were functional during 2010 were provided by M. Abramson, Santa Monica Bay Restoration Foundation.

Weather and sea state are not monitored at Malibu State Beach, necessitating the use of proxy data from nearby localities to evaluate the environmental conditions to which purple sea urchins were exposed during mortality events. Weather, wind, and wave information was based on surface reports for Zuma Beach, California, collected four times daily from 0700 to 1600 h (provided by R. Kittell, National Weather Service). Estimates of the timing and height of tides was based on NOAA tide records for Santa Monica, California. Rainfall and weather information for Los Angeles International Airport (KLAX) was downloaded from MesoWest (<http://mesowest.utah.edu/index.html>) and supplemented with archival records from the Los Angeles Times.

Accounts and photographs provided by numerous observers were used to reconstruct the nature and timing of the events at Malibu Beach. The sources are cited in Findings and Acknowledgements sections, and in figure legends.

## Results

### *Observations on the October 2010 Mass Mortality*

At 0600 h on October 12, 2010, the Los Angeles County Department of Beaches and Harbors (DBH) staff encountered “thousands of small purple sea urchins” at Malibu Lagoon State Beach. The beach maintenance crew disposed of some dead animals and raked others into piles. DBH contacted the Natural History Museum of Los Angeles County for information, out of concern regarding the cause of the mortality.

When I examined the beach on October 14, dead sea urchins were strewn along the high tide line between the Malibu Lagoon and Malibu Pier. Besides *S. purpuratus*, there were small numbers of *S. franciscanus*, approximately 20 *Aplysia vaccaria* Winkler, 1955, and the remains of several crabs (*Loxorhynchus* sp., *Cancer* sp.). DBH personnel said they had never before seen a similar event. They mentioned that the lagoon had breached and drained the previous week but, unaware of the time that the sea urchins died, made no connection between the breach and the mortality. Other individuals on site with whom I spoke at the time, and the news media, suggested that the mortality was related to pollution in the lagoon or to a change in water chemistry. Some explanations offered were manifestly incorrect, such as that dead sea urchins had washed out of the lagoon or had been deposited on the beach by seagulls.

Initially, I anticipated that the sea urchins may have died from one of the diseases that periodically kill *S. purpuratus* and *S. franciscanus*. However, none of the dead animals had the characteristic signs exhibited by diseased strongylocentrotids (Lester et al., 2007). They were desiccated but fairly intact, covered by spines and integument of normal appearance, and many had an unbroken peristomial membrane and Aristotle’s lantern. The vast majority were so little damaged that they obviously had not been killed by predators (e.g. Tegner and Dayton, 1981). However, western gulls (*Larus occidentalis* Audubon, 1839) on the beach were observed probing and removing tissue from dead sea urchins.

To determine the time of the breach and the mortality, I contacted G. Pfeifer, an Ocean Lifeguard Specialist who had worked at the beach for 32 years. His daily log indicated that the lagoon was artificially breached on October 7 at 0930 h, and he recalled that dead sea urchins washed ashore by the morning of October 8. In addition, he mentioned that nearly every year varying numbers of dead sea urchins stranded on shore after the lagoon was breached, but that the most recent mortality was unusually large. Other sources later corroborated his recollections.

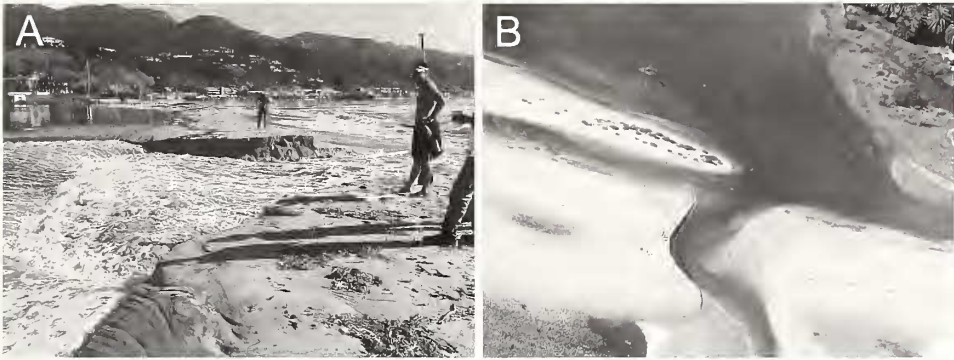


Fig. 2. Breach in the Malibu Lagoon sandbar, which was artificially created on October 7, 2010. A) Water coursing through the berm at 0947 h, shortly after the breach ruptured. B) Aerial view of the southeast portion of Malibu Lagoon on October 7, 2010 at 1315 h, showing a stream of lagoon water running through the breach, across the sandy beach, and onto the intertidal. A field of intertidal cobbles is visible at the lower left. (Photos courtesy H. Burdick, Los Angeles Waterkeeper).

It appears that a chain of events resulting in the mass mortality began on October 6, after the first significant rainstorm of the season. Rainfall in Los Angeles was a record for the date, and discharge from Malibu Creek raised the height and lowered the salinity of water in the lagoon. At Los Angeles Airport, 2.31 cm of rain fell intermittently from 0253 to 1253 h. However, it is not known if rain fell during the low tide ( $-3$  cm at 1458 h) that day on the sea urchins in Malibu's subaerially exposed intertidal zone.

On October 7, a channel was dug illegally across the berm at 0915 h according to State Parks Ranger T. Hayden, who issued a citation to the individual responsible. The excavation was made near the midpoint of the lagoon where the berm was only about 1.5 m wide (Ogle, pers. comm.; Figure 1A). Although the action coincided with a maximum high tide of  $+183$  cm at 0841 h, which raised the level of seawater at the sandbar, water in the rain swollen lagoon created a considerable hydraulic gradient. Lagoon water rapidly liquefied and ruptured the sandbar, releasing a flood of brown, sediment-laden water that swiftly extended seaward from the beach and moved eastward along shore (Ogle and Pfeifer, pers. comm.; Figure 2A). By 1030 h water level in the lagoon dropped 0.6 m (Burdick, pers. comm.), and at 1130 h a "torrent" from the lagoon still roiled the bay (Thompson, pers. comm.). At 1200 h, water continued to pour through the breach, which had by now grown to 1 to 2 m in width, although a great deal of water still remained in the lagoon (Barboza, pers. comm.). As the tide fell in the early afternoon, water from the lagoon streamed toward a central depression in Basin reef and past a layer of sediment deposited by the outflow, which in some places was  $>1$  m high (Ogle, pers. comm.; Figure 1B). An aerial photograph, taken at 1315 h when the tide level was  $+43$  cm, showed lagoon water flowing across the subaerially exposed intertidal (Figure 2B). There were minus tides that afternoon ( $-15$  cm, 1544 h), and for the next 3 days ( $-21$  cm, 1641 h;  $-18$  cm, 1720 h;  $-12$  cm, 1814 h). Thus, immediately after the breach a low tide exposed purple sea urchins to the air and to hyposaline lagoon water that pooled around the individuals situated in depressions on the intertidal shelf. Sea urchins that were immersed in fresh water, or in fresh water mixed with sea water, would have experienced osmotic stress, and the low tides occurring for several days afterwards repeatedly subjected them to heating and desiccation.

Contemporaneously with the breach event, Heal the Bay sondes in the lagoon recorded decreasing water elevations at stations 1 (near the bridge at State Route 1) and 6 (in a western side-branch of the lagoon's main channel), corroborating information provided by observers at the site. Water level began to drop at 0930 h and continued falling until 1900 h, indicating that lagoon water flowed toward the intertidal zone during low tide. Between 0930 and 1830 h the mean and range (in parenthesis) of water quality data recorded at station 6 were: salinity 1.57‰ (1.13–2.23), temperature 21.45 °C (18.32–24.12), Oxygen Reduction Potential 24.24 mV (–152.50–61.70), and pH 7.99 (7.65–8.53). Based on records at Zuma Beach, inshore seawater temperatures were approximately 17.8–21.1 °C, and air temperature during low tide was 17.8 °C. On the afternoon of October 7 and the mornings of October 8 and 9, waves were from the SW and 0.3–0.6 m in height.

On the morning of October 8, less than 24 hours after the breach occurred, large numbers of dead sea urchins were deposited onshore by the rising tide. The following day, considerably more dead animals accumulated on the beach eastward of the lagoon (see Figure 3A, B), and the number of stranded sea urchins was conservatively estimated at 10,000 on a 140 m long segment of the beach (Ogle, Pfeifer, and Ralston, pers. comm.). Over the next several days, prevailing currents moved some dead sea urchins further east toward Malibu Pier, and a small number reached Carbon Beach (Sikich, pers. comm.; pers. obs.; Figure 3C). Western gulls began to feed on dead *S. purpuratus* immediately after they were stranded, and a week later they still scavenged desiccated remains of the sea urchins, usually by removing tissue through the peristomium (Ralston, pers. comm.; pers. obs.; Figures 3D, 4A).

#### *Observations on the October 2011 Mass Mortality*

Two observers who described the mortality event in 2010 as particularly severe, recalled that in previous years dead sea urchins usually washed ashore after the lagoon breached (Pfeifer and Ogle, pers. comm.). However, other individuals familiar with the locality did not recall seeing dead sea urchins at the lagoon after prior breaches, or did not recall seeing significant numbers of dead sea urchins, or remembered only two die-offs of at most 1,000 sea urchins in the previous 10 years. Events in late 2011 provided an opportunity to assess the divergent viewpoints.

The first heavy rainfall of the season on October 5, 2011, which totaled 2.72 cm at Los Angeles Airport, between 0553 and 0753 h, was comparable to the rain accumulation on October 6, 2010. Runoff lowered salinity to 2 to 5‰ at various points in the lagoon where it had been 6‰ the week before (Krug, pers. comm., based on refractometer readings). After 1600 h on October 6, the lagoon was artificially breached (Pfeifer, pers. comm.). Presuming that breaching was timed to avoid detection by the authorities, it probably was accomplished during or after the +152 cm high tide at 1838 h on October 6, and possibly before the +12 cm low tide at 0117 h on October 7. Air temperatures during the period ranged from 14.4 to 15.0 °C, seawater temperatures from 17.2 to 17.8 °C, and 0.6–1.2 m high waves from the SW were recorded at Zuma Beach. The breach, located at the western end of the lagoon near Malibu Colony, directed lagoon water and sediment toward the western flank of Bird Reef, which is exposed to incoming waves from Santa Monica Bay (Figure 1D). Following the breach, daily low tides exceeded datum until October 25.

Dead sea urchins were washed ashore by the morning of October 7 (Pfeifer, pers. comm.), by a rising tide that reached +146 cm at 0746 h; I learned of their presence on



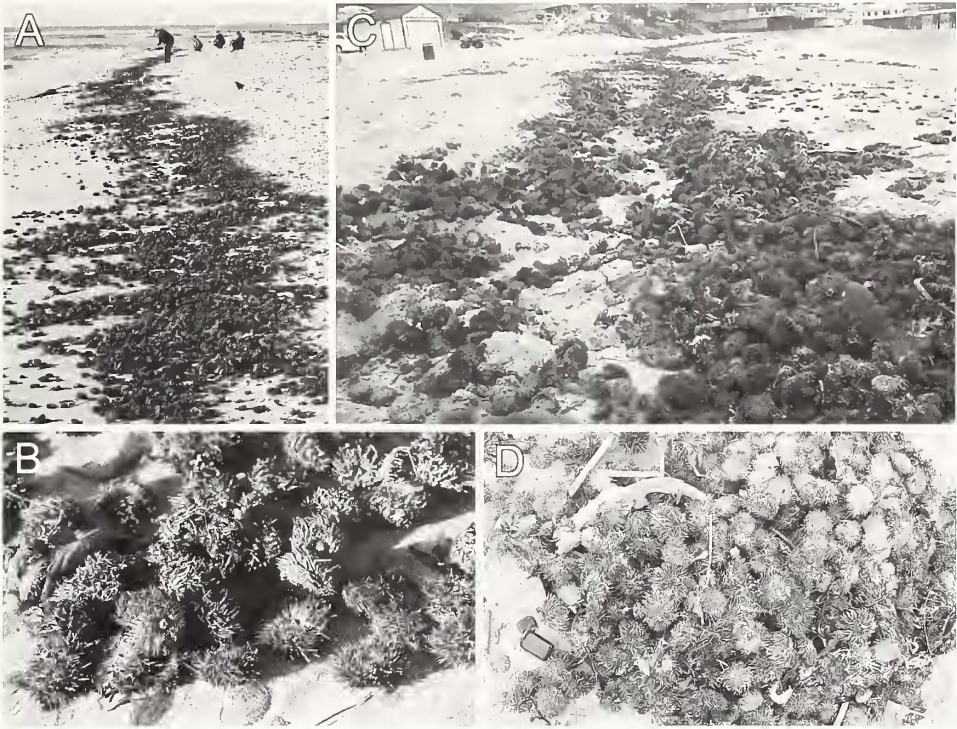


Fig. 3. Sea urchins, primarily *Strongylocentrotus purpuratus*, which were killed in a mass mortality event and stranded on the tideline at Malibu Lagoon State Beach. A) Freshly dead animals deposited by the falling tide on October 9, 2010 at 1519 h. B) Close view of the dead sea urchins in A, which are fully spined and have intact peristomial membrane and Aristotle's lantern. C) Five days after the breach on October 12, 2010, the assemblage of dead animals extends towards Malibu Pier. D) Dead urchins in beach wrack are still largely intact, although spines are missing on some abraded tests on October 14, 2010. (Photos A, B courtesy M. Ralston/AFP, C courtesy D. Murray, Heal the Bay).

October 12 (Krug, pers. comm.). On October 13, six days after the breach, I counted 2,000 dead *S. purpuratus* on the high tide mark between the eastern boundary of Malibu Lagoon and Malibu Pier. Among them were a small number of *S. franciscanus*, a *Pugettia* sp., a *Panulirus* sp. carapace, and a dead cormorant. The mean test diameter of dead *S. purpuratus* in a sample ( $n = 103$ ) haphazardly collected from beach wrack that day, was  $49.8 \pm 6.0$  mm ( $\bar{X} \pm SD$ ). The peristomial membrane and Aristotle's lantern were intact in all but three specimens, and only 24 specimens were partially denuded of spines. Evidently, the relatively undamaged specimens were victims of the mass mortality event. However, one animal was entirely denuded of spines, and the ventral side of the test of two others was broken open. The latter, broken individuals had probably been attacked by sea gulls (Figure 4), as evidenced by the type of damage that they exhibited. Indeed, western gulls were observed scavenging dead urchins on the beach before, during and after the +0.9 cm low tide at 1652 h on that same day. On October 15, before and after a +18 cm low tide at 1811 h, I watched airborne western gulls repeatedly release *S. purpuratus* from their bills, dropping them onto rocks. I also witnessed western gulls in the intertidal zone dislodge and open urchins by penetrating just the peristomium, or by breaking into the ventral or dorsal surface of the test with their bill (Figure 4B–D). Their activities were similar during low tides on October 26–28. Although these observations

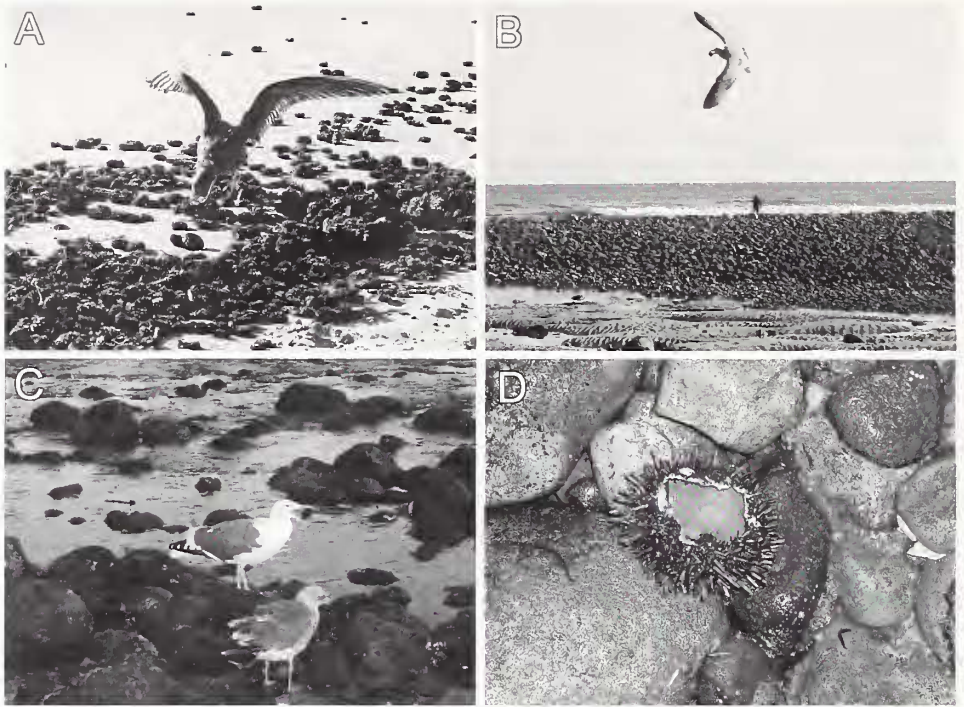


Fig. 4. Examples of predation by western seagulls (*Larus occidentalis*) on purple sea urchins (*Strongylocentrotus purpuratus*) at Malibu Lagoon State Beach. A) *L. occidentalis* feeding on freshly stranded, dead sea urchins on October 9, 2010. B) Airborne *L. occidentalis* attempting to drop and break a sea urchin on intertidal cobbles, October 26, 2011. C) *L. occidentalis* preying on intertidal *S. purpuratus* at dusk on October 15, 2011. D) Remains of *S. purpuratus* eaten by a seagull that fractured the dorsal surface of the test, October 15, 2011. (Photo A, courtesy M. Ralston/AFP).

were made during the first important series of afternoon-minus tides since the previous winter, at a time that numerous *S. purpuratus* might have been expected to be present, few live purple sea urchins were seen in the mid-intertidal. However, many that were found were recent victims of gull predation (Figure 4A-D).

#### Population Density and Size Distribution

On November 7, 2010, a month after the breach, only one living *S. purpuratus* was detected in 60 quadrats surveyed on Basin Reef, which was situated in the path of water discharged from the lagoon. The density ( $\bar{X} \pm SD$ ) of *S. purpuratus* in the quadrats was only  $0.02 \pm 0.13$  per  $0.25 \text{ m}^2$ , and very few additional sea urchins were seen during an examination of the entire reef. Although comparable measurements of the population density at Basin Reef were not made prior to 2010, I was told that local surfers habitually avoided accidental contact with Basin Reef to preclude injuries inflicted by spines of the abundant purple sea urchins living there before the mass mortality (Ogle, pers. comm.). At the same site, after the breach in 2011, 212 animals were found in 113 quadrats surveyed on October 26 and 27, a mean density of  $1.88 \pm 1.12$  sea urchins per  $0.25 \text{ m}^2$ . The statistically significant difference that was found between years, in the density of *S. purpuratus*, suggests that the population at Basin Reef was nearly exterminated in 2010, and recovered in 2011 (Mann-Whitney U test, 2-tailed, corrected for ties:  $U = 2,375.5$ ,

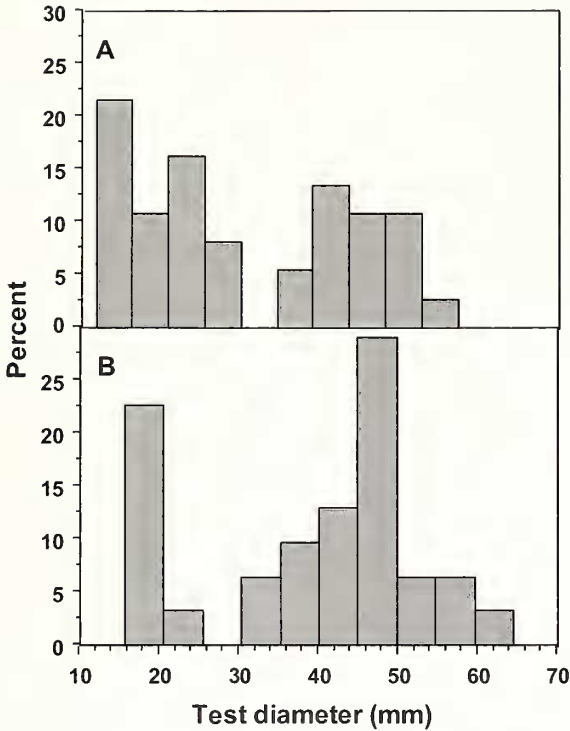


Fig. 5. Size frequency distributions of *Strongylocentrotus purpuratus* collected at Malibu Lagoon State Beach on October 27, 2011, from Basin Reef (A) and Bird Reef (B).

$n = 120$ ,  $P = 0.0013$ ). In 2010, Bird Reef was not exposed to water released by the breach, and there were 277 *S. purpuratus* in the 60 quadrats surveyed there on November 5, a density of  $4.62 \pm 7.72$  per  $0.25 \text{ m}^2$ . However, after Bird Reef was flooded by lagoon water during the breach in 2011, only 73 *S. purpuratus* were found there in 60 quadrats surveyed on October 27, a density of  $1.22 \pm 2.33$  sea urchins per  $0.25 \text{ m}^2$ . The significant difference in population density between years, and the lesser number of *S. purpuratus* found in 2011, suggest that mortality related to the breach had drastically reduced the population density of sea urchins at Bird Reef (Mann-Whitney U test, 2-tailed, corrected for ties:  $U = 5729.5$ ,  $n = 173$ ,  $P < 0.0001$ ).

On October 27, 2011, individuals of *S. purpuratus* were collected from transects at Basin Reef and Bird Reef, and they were measured in order to compare the sizes of animals at these two sites, each of which had been affected by a lagoon breach in a different year. At both reefs the size-frequency distributions of purple sea urchins were bimodal (Figure 5), with the smaller size class probably composed of animals between one and two years of age (year-old *S. purpuratus* are approximately 17 to 33 mm diameter, per Pearse and Pearse, 1975; Rowley, 1990). Purple sea urchins on Basin Reef, where many animals were killed in 2010, were relatively smaller in diameter than those on Bird Reef, where sea urchins were killed by the breach in 2011 ( $30.70 \pm 13.92$  mm test diameter,  $n = 37$  versus  $38.49 \pm 14.23$ ,  $n = 31$  [ $\bar{X} \pm \text{SD}$ ]). The size distribution of animals at Basin Reef could have been shaped by differential size-related mortality in 2010, or by the sizes of sea urchins immigrating to the reef after the die-off. Although adult purple sea urchins are fairly sedentary, they emerge from hiding and move in response to the



availability of food and to the presence of competitors and predators (Paine and Vadas, 1969; Dayton, 1975; Schroeter, 1979; Ebeling et al., 1985; Tegner and Dayton, 1991). It is possible that the predominant, larger size class of purple sea urchins at Bird Reef, which were survivors of the 2010 and 2011 mortality events, inhibited the immigration of smaller animals, or perhaps more likely that disproportionately more small animals died during the mortality event. Although the relatively large mean size (49.8 mm diameter) of dead purple sea urchins found in beach wrack argues against the latter interpretation, it also suggests a possibility that small individuals were more readily destroyed or that large animals were preferentially transported ashore.

### Discussion

#### *Mass Mortality of S. purpuratus at Malibu*

The behavior and physiology of *S. purpuratus* were not directly monitored during and immediately after the population was exposed to lagoon discharge. Also, meteorological and oceanographic conditions and the chemistry of water in the lagoon and the bay were not comprehensively monitored at Malibu Lagoon State Beach during mass mortality events in 2010 and 2011. As a consequence the cause of the die-offs cannot be determined with certainty, but causative factors can be inferred from the information that is available.

It is notable that the only freshly dead marine animals that were found in significant numbers at Malibu were *S. purpuratus* and *S. franciscanus*. Other animals deposited among the sea urchins on the beach were so rare that their occurrence seems unrelated to the mass mortality. The small number of dead *Aplysia vaccaria* seen in 2010 were likely senescent individuals, as this species is an annual (Audesirk, 1979; Angeloni et al. 1999). Sea urchins alone seem to have been affected, suggesting that they were more susceptible than other organisms to the causative agent(s). In addition, so many individuals of *S. purpuratus* were killed compared to *S. franciscanus* that it appears the phenomenon was restricted to the intertidal zone where the numbers of *S. purpuratus* far exceed those of *S. franciscanus*, which is primarily a subtidal species in southern California.

Circumstances of the mass mortality events in 2010 and 2011 were consistent with the hypothesis that the sea urchins were killed by brackish water released through breaches in the lagoon. In both instances, dead sea urchins appeared two days after the first major rainfall of the annual rainy season and one day after the lagoon was breached. In both instances dead animals were deposited down-current from the breach. In both instances it appeared that the population density of *S. purpuratus* was reduced on the reef closest to outflow from the lagoon, and that the population recovered to some extent within a year. Parallels between events indicate that in both cases sea urchins were killed by the same agents. However, differences in the extent of mortality between years suggest that several interacting factors were involved.

Based on the literature (reviewed in the Introduction), the physical factors most often associated with mass mortality of *S. purpuratus* included exposure to elevated temperature  $\geq 23.5$  °C, or to reduced salinity  $\leq 21$ ‰, for several hours. Since the salinity of water released from the lagoon was only 1 to 5‰ in 2010 and 2011, it could well have injured or killed individuals of *S. purpuratus*, even if its salinity were moderately elevated by an admixture of seawater. Ambient temperature was unlikely to have been injurious, since nearshore air and water temperatures were below lethal levels in both years. Although water temperatures  $\geq 23.5$  °C were recorded in the lagoon for 2 h during



the 2010 breach, water leaving the lagoon would have cooled after exposure to the air and to sea water.

Other stressors that are potentially deleterious to *S. purpuratus* include hypoxia, toxic pollutants, emersion, and rapid burial and smothering in sediment (i.e., obrution). *Strongylocentrotus purpuratus* is resistant to hypoxic conditions (Johansen and Vadas, 1967; Burnett et al., 2002), but immersion in strongly hypoxic or anoxic lagoon water might have increased the susceptibility of individuals to osmotic stress. Dissolved oxygen (DO) concentration in the lagoon was not recorded during the interval encompassing the mortality events (Abramson, pers. comm.), but it had in the past ranged from  $< 1 \text{ mg L}^{-1}$  nearly to saturation (2NDNATURE, 2010). Even so, hypoxic lagoon water would have been aerated while flowing toward the intertidal zone. The lagoon water contains a variety of inorganic and organic pollutants, fecal bacteria, and pathogens (Ambrose and Orme, 2000; Dagit et al., 2009; BenVau, 2011), and it is possible that urban runoff from the season's initial storm contributed a concentrated "first flush" of contaminants to the lagoon. However, toxic contaminants are not seriously elevated at the site (Schiff and Bay, 2003), and a die-off of the fauna within the lagoon did not coincide with the mass mortality of intertidal sea urchins. Therefore it is unlikely that a transitory exposure to pollutants killed *S. purpuratus*. Conversely, Schroeter (1978) found that multi-day series of minus tides can weaken or kill *S. purpuratus* through exposure to desiccation, sunlight, and elevated temperatures. Although it is difficult to precisely relate Schroeter's experimental results to die-offs at Malibu, it is notable that the episode in 2010 was accompanied by a series of minus tides. In contrast, conditions in 2011 may have been relatively less stressful, accounting for the lower mortality of *S. purpuratus* that year, because the event occurred during plus tides and was preceded by 6 days without minus tides. Following the breaches, some sea urchins may have been killed by rapid burial in sediment, but direct evidence is lacking. Although a considerable amount of sediment from the breach was deposited on the intertidal shelf, waves and currents redistributed it before the reefs were examined.

#### *Mass Mortality of S. purpuratus in California*

The catastrophic natural events, which are reviewed in the Introduction, are not the only agents of massive sea urchin kills. Humans have profoundly altered the population size of *S. purpuratus* throughout its range, often through their efforts to harvest or to eradicate sea urchins. In that respect, the mass mortalities of *S. purpuratus* at Malibu Lagoon State Park are exceptional, as they were human-caused but unintentional. They appear to have been "collateral damage" stemming from attempts to improve conditions for recreational surfing.

Paleoindians, who were the first Californians to fish for strongylocentrotid sea urchins, unwittingly initiated a 10,000-year interaction with *S. purpuratus* that has often been detrimental to the species. After Paleoindians overharvested sea otters (*Eulydra lutris* (Linnaeus, 1758)) and sheephead wrasse (*Seimicosyplus pulcher* (Ayres, 1854)), eliminating the predators that had held *Strongylocentrotus* populations in check, sea urchins became a notable component of the fishers' diet (Salls, 1995; Erlandson et al., 2005; Erlandson et al., 2011).

During historical times Californians conspicuously boosted the population growth of *S. purpuratus* at least twice. In the first instance, well before 1900, sea otters between Alaska and Mexico were hunted almost to extinction by fur traders (Riedman and Estes, 1988), and absent their chief predator, sea urchins are thought to have proliferated

(Dayton et al., 1998; Tegner and Dayton, 2000; Foster and Schiel, 1988, 2010). A second population surge of purple sea urchins occurred during the 1950s, when enormous volumes of untreated sewage were discharged by metropolitan Los Angeles and San Diego. Despite the influx of toxic pollutants, sea urchins thrived on the nutrients released at sewage outfalls in southern California (North, 1974).

In response to marked increases in the numbers of *S. franciscanus* and *S. purpuratus*, concerted efforts have been made to eradicate strongylocentrotids that were deemed undesirable by the kelp-harvesting industry and various fishing interests. Beginning in the 1970s groups of divers armed with hammers smashed sea urchins, and boats spread hundreds of tons of quicklime (calcium oxide) on concentrations of sea urchins, killing them and other fauna. Temporarily exterminating sea urchins may have enhanced the recruitment rate of giant kelp (*Macrocystis pyrifera*) locally, but widespread recovery of kelp beds did not occur before large-scale upgrades of sewage treatment facilities extensively improved water quality (North, 1974; Foster and Schiel, 2010; Meux and Ford, 2010).

A subsistence fishery persisting in the 20<sup>th</sup> Century among Native American and immigrant populations on the West Coast reduced the numbers of *S. purpuratus* to some extent (Johnson and Snook, 1935; Greengo, 1952; Heizer and Mills, 1952; Kato and Schroeter, 1985). Some purple sea urchins have also been damaged and removed through human recreational activities (Addessi, 1994; Murray et al., 1999). In contrast, a commercial fishery initiated in the early 1970s had an extensive and long-lasting impact (Kato, 1972; Kalvass and Hendrix, 1997; Parker and Ebert, 2004). In California, old-growth stocks of *S. franciscanus* were depleted and populations collapsed, because “until the late 1980’s, the sea urchin fishery was not actively managed...” (Kalvass and Hendrix, 1997:13; Rogers-Bennett, 2007). Fortunately for *S. purpuratus*, nearly 99% of the commercial harvest consisted of *S. franciscanus*, and localized removal of red sea urchins may have enhanced the access of purple urchins to food and habitat (Schroeter, 1978; Parker and Ebert, 2004).

### Conclusions

Based on available information, recent mass mortalities of sea urchins at Malibu Lagoon State Beach appear to have been the indirect result of human-caused breaches in the sand bar, a previously unreported source of sea urchin mortality. The presumed cause of death, exposure to low-salinity water, has affected populations of *S. purpuratus* elsewhere (MacGinitie, 1939; Sousa, 1979; Littler and Littler, 1987; Ebert and Grupe, 2008). At Malibu, *S. purpuratus* and *S. franciscanus* seem to have been the only animals killed by the breaches, but that could not be confirmed. Perhaps particular hydrodynamic characteristics of dead purple sea urchins (Denny and Gaylord, 1996; Stewart and Britten-Simmons, 2011) favored their massive accumulation on the tide line. At other localities, freshly killed mollusks and polychaetes have been stranded during storms (Rees et al., 1977), but none washed ashore at Malibu. However, they or other animals that were killed could have been transported offshore, as sometimes occurs following intertidal mass mortalities (e.g., Hendler, 1977; Girard et al., 2012, and pers. comm.).

No evidence was found that *S. purpuratus* died because of elevated temperature or disease. Hypoxia, hydrogen sulfide, toxic pollutants, or rapid burial in sediment may have played a role in the mortality events, but crucial facts regarding water chemistry and sediment deposition are lacking, as is information regarding the tolerance of adult purple

sea urchins to physical and chemical stressors acting singly and in combination. Thus, a critical understanding of the periodic die-offs at Malibu requires further research on the behavior, physiology, and population dynamics of *S. purpuratus*, in addition to long-term monitoring of breach incidents and water quality at the lagoon.

Mortality events in 2010 and in 2011 occurred in early October, after storms that produced similarly heavy rainfall. Since it is likely that nearly equal volumes of brackish water were released from the lagoon in both events, why were ten times more *S. purpuratus* killed in 2010? In that year, at low tide, lagoon water flowed directly toward the central depression in Basin Reef, where the seaward edge of the shelf could have deterred marine water from mixing with hyposaline lagoon water and thereby mitigating its harmful effects. Consequently, in 2010, discharge from the lagoon coinciding with a diurnal minus tide, simultaneously exposed *S. purpuratus* to hyposaline water, sunlight, and dehydration for an extended period. Additionally, after emersion, purple sea urchins replace fluid in their digestive tract with air, using the inflated gut for gas exchange (Burnett et al., 2002). Having an air-filled gut may have increased their susceptibility to osmotic shock and also made them somewhat buoyant, a possibility which should be experimentally tested. Repeated exposure during several more minus tides may have resulted in the influx of additional dead sea urchins that occurred two days after the breach in 2010. In contrast, in 2011, *S. purpuratus* was subjected to less stress because Bird Reef did not impound freshwater outflow from the lagoon, and because the series of low tides subsequent to the breach were above datum. Regarding the 2011 event, timing of the breach relative to the low tide is not known.

The paucity of sea urchins found in the mid-intertidal at Malibu Lagoon State Beach was to some extent a result of seagull predation. When the beach was surveyed, western gulls repeatedly were seen attacking sea urchins on the crests of subaerially exposed reefs and around partially submerged cobbles. Their behavior resembled the birds observed at Palos Verdes Peninsula described by Snellen et al. (2007). The authors estimated that one western gull potentially could consume 3,229 *S. purpuratus* each year, and that the flock of ~45 birds that they studied could consume 145,305 sea urchins. Since greater numbers of western gulls occur at Malibu, their impact on the sea urchin population could be considerable. Moreover, similarly to the “trophic cascade” created by glaucous-winged gulls (*Larus glaucesceus* Naumann, 1840) in Washington (Wootton, 1997), western gulls might indirectly increase the growth of intertidal algae at Malibu, by reducing the amount of sea urchin herbivory.

In the past, severe storms may have periodically devastated the intertidal population of *S. purpuratus* at Malibu Lagoon, as in 1998 when historic photographs (Schwarz and Orme, 2005: Figs. 6, 7) show that a remarkable El Niño event blanketed the intertidal zone with sand. However, repetitive mass mortalities at Malibu Lagoon, due to natural and artificial breaches and gull predation, appear to maintain the intertidal population of purple sea urchins at consistently low density. Population densities of *S. purpuratus* vary markedly depending on configuration and composition of the benthic substrate (Sagarin and Gaines, 2002; Ebert, 2010). Nevertheless, density of *S. purpuratus* at Malibu Lagoon is low compared to other southern California intertidal localities where 20 to 100+ individuals per m<sup>2</sup> quite often are found (Schroeter, 1978; Littler and Littler, 1987, Lawrenz-Miller, pers. comm.). Since *S. purpuratus* is an “ecosystem engineer,” and since its grazing controls algal and invertebrate community structure in southern California (Ebert, 1977; Sousa et al., 1981; Rogers-Bennett, 2007:415), the low population density at Malibu may appreciably affect intertidal ecology of that locale.